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Correlates of home range sizes of giraffes, *Giraffa camelopardalis*

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Abiotic, biotic and human influences are factors that can affect animal home ranges. We calculated home range sizes of adult giraffes in the Tarangire-Manyara region of northern Tanzania (N = 132 giraffes with data collected over 6 years), and investigated correlations between home range sizes and environmental and anthropogenic factors (for a subset of N = 71 giraffes). We used a 95% kernel utilization distribution to define home ranges and modelled home range size as a function of environmental and anthropogenic predictors using multiple linear regression and model selection. We also computed home range sizes of giraffes using 100% minimum convex polygons to compare with estimates from previously published studies, and tested the relationship between rainfall and home range sizes of giraffes across Africa. Average kernel home range sizes were 114.6 km^2 for females (N = 109) and 157.2 km^2 for males (N = 23). Adult female giraffe home range sizes (N = 67) were negatively correlated with distance to densely populated towns. Females living closer to towns had significantly larger home ranges, suggesting a need to range farther to avoid human-impacted areas while obtaining critical resources. No such relationship was evident with bomas, which are homesteads built by indigenous pastoralist people, suggesting that female giraffes are tolerant of traditional land uses. Mean annual rainfall explained 74% of the variation in home range sizes of giraffes across the African continent, with smaller home ranges in regions with higher rainfall and thus greater productivity, providing additional evidence that access to critical resources mediates home range size of this megaherbivore. Quantifying home range sizes and identifying ecological and anthropogenic factors affecting space use can provide insights into mechanisms driving use of space and help wildlife managers make informed decisions that improve conservation plans for at-risk species such as giraffes.

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An important concept that describes space use by animals is the home range, the spatial extent over which an animal repeatedly travels in search of food and mates and to care for young (Burt, 1943). Home range behaviour is assumed to be an expression of an animal's decision-making process, shaped by natural selection, to access spatially dispersed resources in a manner that increases fitness (Börger et al., 2008; McLoughlin et al., 2007; Mitchell & Powell, 2004; Powell & Mitchell, 2012; Schoepf et al., 2015). Landscapes tend to be spatially heterogeneous, so the amount of space used by an individual is partially dependent upon the type, abundance and composition of resources across the landscape (Dechen Quinn et al., 2013; Ofstad et al., 2016; Saïd & Servanty, 2005). Energy is required to access those resources; therefore, space use consists of a trade-off between acquiring resources and expending energy (Fretwell & Lucas, 1970). Overall, animals theoretically should occupy the smallest area that contains the required resources (Harestad & Bunnell, 1979).

Ungulates are a diverse group of large herbivores that have a profound impact on plant populations, vegetation structure and ecosystem processes (Ofstad et al., 2016). The structure and function of East African savannah ecosystems are reliant upon intact communities of ungulates, as these mammalian herbivores consume about half of all plant production and are important prey for predators and scavengers (du Toit & Cumming, 1999; Shorrocks, 2007). However, most studies of ungulate home range ecology are from temperate regions (Ofstad et al., 2016). Home range sizes of ungulates in temperate regions are influenced by biotic factors including the configuration of habitat within the landscape (Cibien & Sempere, 1989; Saïd et al., 2005; Saïd & Servanty, 2005; Tufto et al., 1996), an individual's sex, age (Cederlund & Sand, 1994; Relyea et al., 2000) and body weight (Harestad & Bunnell, 1979), and by abiotic factors such as climate and season (Morellet et al., 2013), the species' local population density

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(Kjellander et al., 2004) and human impacts (Dechen Quinn et al., 2013). Quantifying biotic and abiotic drivers of home range behaviour of ungulates in African savannahs can advance our understanding of tropical species and the elements they require to survive and reproduce. In addition, by quantifying home range sizes and identifying ecological and anthropogenic factors affecting space use, wildlife managers can make informed decisions that improve conservation plans for at-risk species (Deacon & Smit, 2017).

Giraffes, *Giraffa camelopardalis*, are endemic African ruminant ungulates, and one of only a handful of extant terrestrial megaherbivore species (Owen-Smith, 1988). Giraffes are nonterritorial, resident browsers that feed mostly on leaves, twigs, flowers and fruits of woody plants (Dagg, 2014). The species plays a major role in shaping the vegetation of savannah ecosystems (Strauss et al., 2015). Africa-wide, most populations of giraffes have declined in recent decades (Muller et al., 2018). Quantifying spatial ecology and landscape use by giraffes is critical for developing effective conservation measures (Deacon & Smit, 2017). Several studies have reported home range sizes for giraffes throughout the species' range (Berry, 1978; Deacon & Smit, 2017; du Toit, 1990; Fennessy, 2009; Le Pendu & Ciofolo, 1999; Leuthold & Leuthold, 1978; van der Jeugd & Prins, 2000), but these estimates varied substantially (Table 1). Abiotic, biotic and human influences are likely to be contributing factors that affect home range sizes of giraffes, yet ecological and anthropogenic influences that might underlie giraffe space use have not been quantitatively analysed.

Our first objective was to calculate year-round home range sizes of adult Masai giraffes, *G. c. tippelskirchi*, from a free-ranging population in the Tarangire-Manyara Ecosystem of northern Tanzania. This ecosystem consists of a mix of vegetation types, as well as of protected and unprotected lands.

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Second, we examined correlations between individual home range size and environmental and anthropogenic factors at an ecosystem scale in a spatially heterogeneous study area (~1500 km^2) to better understand potential mechanisms driving space use of this threatened megaherbivore. We specifically tested whether giraffes with a greater amount of closed habitat in their home ranges have smaller home range sizes, as denser vegetation offers both food and cover (Ofstad et al., 2016). We also predicted that home range sizes of giraffes living closer to human habitation would be larger because the human-impacted landscape in this study area is fragmented by agriculture and fuelwood cutting (Msoffe et al., 2011) and bushmeat poaching is widespread (Kiffner et al., 2015). Finally, we tested whether males had larger home ranges than females as their life-history strategy involves roaming among herds seeking adult females in oestrus (Dagg, 2014). Home ranges can change due to factors such as seasonal movements (Morellet et al., 2013), so it is important for robust analyses to ensure that home range estimates have stabilized. Therefore, we performed a bootstrap procedure to assess home range stabilization given each individual's sample size of locations and used only the subsample of giraffes whose home range estimate stabilized (Tingley et al., 2014).

Our third objective was to compare home range estimates from our study area with published data from giraffe populations across Africa, and to test the relationship between giraffe home range size and mean annual rainfall at the continental scale as a potential explanation for observed variation in space use among populations.

<H1> METHODS

<H2>Study Site

The study area was located in northern Tanzania, East Africa. We sampled a 1500 km^2 area that included parts of Tarangire and Lake Manyara National Parks and the entirety of Manyara

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Ranch Conservancy (Fig. 1). The 2850 km^2 Tarangire National Park is the largest protected area in the region (Lamprey, 1963). Our giraffe survey area encompassed the northern half of the park. Manyara Ranch Conservancy, located 3 km north of Tarangire National Park, is a private 140 km^2 ranch dedicated to tourism and habitat conservation. Lake Manyara National Park, in the west of the study area, spans a 330 km^2 area between the alkaline Lake Manyara and a steep rift wall, of which we surveyed the northern two-thirds. The mean altitude of the region is approximately 1000 m above sea level.

The study area consists of a savannah biome with variation in vegetation types ranging from open grasslands to dense deciduous bushlands and thickets (Lamprey, 1963). The Makuyuni and Tarangire Rivers and associated waterholes, together with several streams flowing down the rift wall into Lake Manyara, provide year-round access to water for wildlife. The landscape connecting the three reserves is fragmented by roads, villages and agricultural land, but the study population of giraffes is still considered a functioning metapopulation as all reserves are connected by movements of adult females (Lee & Bolger, 2017).

<H2>Data Collection

<H3>Giraffe locations

During 2011–2016, we conducted 31 photographic capture–recapture surveys during which we systematically searched for giraffes along all dirt roads in the study area. Each sampling occasion consisted of two back-to-back surveys (surveys were done by M.L.B. and D.E.L.), or sampling events, conducted towards the end of every precipitation period (short rains = February; long rains = June; dry = October) and separated by 4-month intervals. During each sampling event, individuals were either ‘captured’ or ‘recaptured’ by slowly approaching and photographing the animal’s right side from approximately 150 m at a perpendicular angle

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(Canon 40D and Rebel T2i cameras with Canon Ultrasonic IS 100–400 mm lens, Canon U.S.A., Inc., One Canon Park, Melville, New York, NY, U.S.A.). We identified individual giraffes from the photographs using their unique and unchanging coat patterns (Dagg, 2014; Foster, 1966) with the aid of pattern-recognition software Wild-ID (Bolger et al., 2012). We also recorded every individual's geographical coordinates, sex and age class. We used several physical characteristics to categorize giraffes into the three age classes: calf, subadult or adult (adults were at least 3 years old, according to Strauss et al., 2015). Successive relocation points were separated by ≥10 days; thus, we expected minimal autocorrelation for home range estimation (Fieberg, 2007).

We carried out the field research with permission from the Tanzania Commission for Science and Technology (COSTECH), Tanzania National Parks (TANAPA), the Tanzania Wildlife Research Institute (TAWIRI), African Wildlife Foundation and Manyara Ranch Conservancy.

<H3>Environmental and anthropogenic covariates

We hypothesized that giraffe home range sizes were correlated with covariates: (1) proportion of vegetation types in the home range; (2) distance of home range from human settlements; (3) density of survey routes in the home range; (4) sex of the individual; and (5) local giraffe population density. We included giraffe population density (for estimation see below) as a factor because it is known to influence home range sizes of mammals (Kjellander et al., 2004; Schoepf et al., 2015).

We derived four vegetation types from a natural vegetation map developed by the University of Copenhagen's Vegetation and Climate Change in Eastern Africa (VECEA) project (downloaded from http://vegetationmap4africa.org/2_Vegetation_map.html). Representing

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closed to open habitats, categories included (1) deciduous bushland and thicket, (2) wooded grassland, (3) edaphic grassland on volcanic soils with scattered woody species and (4) edaphic grassland on drainage-impeded or seasonally flooded soils (Kindt et al., 2011). We mapped human-developed areas and bomas using Google Earth imagery. Bomas were small temporary family settlements built by members of the pastoralist Masai tribe that consisted of huts made of mud or cow dung, whereas developed areas were more densely populated towns with permanent concrete structures (Fig. 1).

We calculated local giraffe population density by dividing the number of adult giraffes by surveyed area (km^2) of each site, with surveyed area calculated as the minimum convex polygon enclosing the surveyed route network in each site, plus a boundary strip 500 m wide (Parmenter et al., 2003).

<H2>Data Analysis

<H3>Home range size

We estimated year-round home range sizes of adult (>3 years old) male and female giraffes by combining multiple years of relocations for each individual. Calves and subadult giraffes were not included in this analysis as natal dispersal may bias home range size, and home ranges of calves are not independent of the home range of their mothers. We applied two different calculation methods to generate home ranges: the 100% minimum convex polygon (MCP) for comparison with previously published studies and the 95% utilization distribution (UD) with a kernel density estimator (Seaman & Powell, 1996) for testing predictions about home range correlates. Rather than drawing polygons around observed locations to create a minimum convex polygon, utilization distributions are density functions that describe the probability of an animal being present in an area (Jennrich & Turner, 1969). Börger et al. (2006) found the kernel method

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was the most unbiased home range estimator across sampling regimes and was robust to relatively smaller sample sizes, so we used this method to generate home ranges for our correlation analysis.

We employed a two-step process to estimate robust home range sizes by kernel density. For kernel density estimators, the choice of a smoothing parameter or bandwidth (h), can substantially affect results (Fieberg, 2007). If h is set too small, home ranges consists of patches around every location, but if h is set too large, then the home range border is placed far from the actual locations. First, to calculate the optimal bandwidth, we generated home ranges with a variety of h values and determined that $h = 1500$ provided the most reasonable configurations. We also generated home ranges with both 75% and 95% kernel utilization distributions (kernel UD). The 75% kernel UD excluded locations furthest from the core, which we believed underestimated the home range size. We therefore proceeded by using 95% kernel UD with $h = 1500$ for final analyses.

Second, to determine whether an individual giraffe's 95% kernel UD home range estimate stabilized and was thus robust, we ran a bootstrapping algorithm in which, for each individual, we drew at random an increasing number of its relocation points and estimated the 95% kernel UD with each successive addition of a location (Tingley et al., 2014). We began by considering only adult giraffes with a minimum of 10 resights. We then generated home range estimates, starting with five randomly selected locations and successively integrating the remaining locations at random. We repeated the procedure 50 times per giraffe and calculated the mean change in home range size per added location. We inspected the graphs of change in home range size and considered the home range estimate to have stabilized when at least three successively added locations resulted in estimates with a <5 km change in area (e.g. Fig. 2). For the

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subsequent analysis of environmental and anthropogenic correlates of home range size, we used the subset of giraffes with stabilized home range estimates. We also added boundaries where the landscape acted as a barrier on giraffe movement for improved home range estimation and reduction of type II errors (Calenge, 2006; Fieberg & Börger, 2012). These barriers were the Lake Manyara shoreline, a rift wall in the western part of Lake Manyara National Park, and agricultural land between Tarangire National Park and Manyara Ranch Conservancy (e.g. Fig. 3). We calculated all home range sizes using the package adehabitatHR (Calenge, 2006) in R (version 3.4.2).

<H3>Home range covariates

In our analysis of ecological and anthropogenic correlates to home range size, we used only the subsample of giraffes residing in the northern part of Tarangire National Park and in Manyara Ranch Conservancy, because these areas had higher survey route coverage with respect to average giraffe home range size (Fig. 1). We were thus confident that our sample of giraffe home ranges did not extend significantly beyond our survey area. We also excluded giraffes living in Lake Manyara National Park because this park is relatively small, nearly isolated and contains little variation in vegetation.

We generated distances to human settlements by calculating the smallest distance from the edge of each individual's 100% MCP home range to both the nearest developed area and the nearest boma, using the function 'gDistance' in the R package 'rgeos' (Bivand, 2018). We calculated the proportions of different vegetation types within each giraffe's 95% kernel UD home range (which included a larger area surrounding giraffe relocations than MCP, see Results) using the function 'intersect' in the R package 'raster' (Hijmans & van Etten, 2012). The same procedure was conducted for survey route coverage, where kilometres of roads per area (km^2)

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were calculated for each 95% kernel UD home range with the 'intersect' function from R package 'raster' (Hijmans & van Etten, 2012).

We used multiple linear regression and model selection to determine which variables best explained variation in log-transformed home range sizes of giraffes in our sample. Explanatory variables included sex, proportion of four vegetation types, distance from both bomas and towns, and local giraffe population density (see Table 2 for variables). We also tested models with interactions between sex and giraffe population density, and sex and distance to towns. We developed and compared a suite of 14 a priori models reflecting various combinations of explanatory variables, including a null and global model. We used Akaike information criterion corrected for small sample sizes (AIC_c; Burnham & Anderson, 2002) and AIC weights (w_i) for model selection and model averaging. We considered models with $AIC_c < 2$ to be competitive, and we examined the degree to which 95% confidence intervals of the beta coefficients (ß) included 0 to determine the direction and precision of evidence for covariate effects. To account for model-selection uncertainty, we calculated model-averaged ß estimates and 95% confidence intervals by averaging from all weighted models and assuming ß = 0 for models in which an explanatory variable did not appear (Burnham & Anderson, 2002). We conducted model selection and averaging using the package MuMIn for R (Barton, 2018).

We collated mean home range estimates of adult male and female giraffes throughout the range of the species and obtained data on mean annual rainfall (mm) in each study area, from published sources. We conducted a simple linear regression analysis testing the effect of rainfall on mean log-transformed MCP home range sizes of both sexes combined. We used MCP because all but one of the previous studies estimated home range sizes using this method.

<H1>RESULTS

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We identified 1264 individual adult giraffes in the Tarangire-Manyara Ecosystem using photographic capture–mark–recapture methods. The bootstrapping procedure indicated that estimates of home range sizes stabilized for 132 giraffes (109 females and 23 males). We reported home range sizes for these individuals. Home range sizes of giraffes whose home range estimates stabilized did not differ significantly from home range sizes of giraffes whose estimates did not stabilize (Welch's two-sample *t* test: t_{245}= -1.25, P = 0.212), thus our sample was not biased towards individuals with smaller or larger home range sizes. Further subsetting of the data set by including only giraffes residing in Manyara Ranch Conservancy and northern Tarangire National Park resulted in a sample of 71 individuals (67 females and 4 males) that we used for testing correlates of home range size. The mean number of locations per giraffe in the final subset was 16.3 (SD = 3.06, range 10–24 locations).

Overall mean home range sizes (95% kernel UD, h = 1500) for giraffes in Tarangire and Lake Manyara National Parks and Manyara Ranch was 122.0 km^2 (SE = 50.8 km^2, N = 132), with a mean of 114.6 km^2 (SD = 49.0 km^2, N = 109) for females and 157.2 km^2 (SD = 44.9 km^2, N = 23) for males. Home range sizes of males were significantly larger than those of females (Welch's two-sample *t* test: t_{34} = -4.07, P < 0.0003). Mean 100% MCP home range sizes measured 24.1 km^2 (SD = 19.7 km^2), with a mean estimate of 23.3 km^2 (SD = 20.1 km^2) for females and 27.8 km^2 (SD = 17.7 km^2) for males, with no significant difference in size between males and females (t_{35} = -1.08, P = 0.288). The home ranges computed with minimum convex polygons were substantially smaller than with kernel density estimators, especially if resights occurred primarily along one survey route in a linear shape (e.g. Fig. 3). Table 1 reports site-specific home range sizes for 67 females and 4 males in Tarangire National Park and Manyara Ranch Conservancy, and for 29 females and 8 males in Lake Manyara National Park, along with

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previously reported giraffe home range sizes throughout Africa from the literature.

In our multiple linear regression analysis testing ecological and anthropogenic correlates of log-transformed home range size, regression diagnostics indicated that the dependent variable home range size was normally distributed and linearly related to the predictor values. Four models were competitive (<2 ΔAIC_c) and five models together carried 99% of weight (Table 2). The top-ranked linear regression model explaining variation in home range sizes of giraffes included developed areas (towns) ($P < 0.001$) and survey route density ($P = 0.051$), and this model carried more than twice the weight of the next-ranked model (Table 2). The predictors in the top model explained 19% of the variance in home ranges size ($R^2 = 0.191$, $P < 0.001$). Model-averaged beta coefficients (Table 3) from all models carrying weight demonstrated a negative relationship between home range size and distance to towns (ß = -0.088, SE = 0.037, $P = 0.019$; Fig. 4), with no other significant explanatory variables.

Simple linear regression analysis of data from published studies throughout Africa indicated a significant negative correlation between mean annual rainfall in a study area and mean log of 100% MCP home range sizes of giraffes ($F_{1,8} = 26.25$, $P < 0.001$; Fig. 5). Regression diagnostics demonstrated that the dependent variable home range size was normally distributed and linearly related to the explanatory variable rainfall. This relationship explained a large proportion of variation in home range sizes throughout the range of the species ($R^2 = 0.74$).

<H1>DISCUSSION

We found that home range sizes of adult female Masai giraffes at an ecosystem scale were significantly larger in areas closer to towns with high densities of humans compared with surrounding landscapes. Vegetation type, local giraffe population densities and distance to traditional pastoralist family compounds (bomas) had no significant influence on space use by

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giraffes in our study area. Throughout Africa, home range sizes of adult giraffes significantly decreased with increasing mean annual rainfall.

<H2>Ecological and Anthropogenic Correlates of Home Range Size

Our analysis of anthropogenic and ecological correlates of individual home range sizes in the Tarangire-Manyara Ecosystem indicated that use of space by giraffes was influenced primarily by the individual's proximity to densely populated towns (Fig. 4). The farther from developed human areas, the smaller the giraffe home range size—but no such correlation was evident with bomas, which are dispersed family homesteads built by members of the pastoralist Masai tribe. Contrary to our predictions based on determinants of home range sizes for other ungulate species, home range sizes of giraffes were not significantly correlated with vegetation type or local giraffe population density. Kjellander et al. (2004) hypothesized that conspecifics will compete for local resources and thus limit each other's use of space when densities are high, resulting in smaller individual home ranges. However, we did not observe this in our study.

As expected, giraffes living closer to densely populated towns had significantly larger home range sizes, indicating a need to travel greater distances to obtain critical resources while avoiding human disturbance. Kie et al. (2002) noted that in landscapes where habitats are less interspersed, large herbivores must travel longer distances to the nearest patches of suitable habitat once forage is depleted or because of anthropogenic disturbance (including human predation risk). This increased expenditure of energy might play a role in the lower survival and population growth rates of giraffes observed outside protected national parks in this study area (Lee & Bolger, 2017; Lee et al., 2016). Indeed, habitat fragmentation caused by logging was correlated with larger home range sizes and subsequent reduced fitness of spotted owls, *Strix occidentalis*, in forests of the western United States (Carey et al., 1990; Glenn et al., 2004); thus,

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patterns of home range size may offer proxy measures for evaluating habitat quality. Giraffe habitat tends to be degraded or lost near dense areas of human habitation, as people often cut trees for fuelwood and much of the landscape surrounding towns has been converted to agriculture. However, no such negative relationship with home range size was observed with distance to bomas, suggesting either that traditional land uses as practiced by nomadic pastoralists do not adversely affect use of space by adult female giraffes, or that space use by giraffes is a function of human population density. Anthropogenic disturbances leading to habitat loss and fragmentation are among the biggest threats to global biodiversity (Lindenmayer & Fischer, 2013). Land-use planning and zoning that takes into consideration the needs of large herbivores can help sustain populations in increasingly human-dominated landscapes (Lee, 2018; Lee & Bond, 2018).

The 95% kernel UD (utilization distribution) home ranges of 23 males were significantly larger than ranges of 109 females in the entire Tarangire-Manyara study area. This result is similar to the only other study of giraffe home ranges to utilize kernel estimators, for reticulated giraffes, *G. c. reticulata*, in Kenya (VanderWaal et al., 2014). Adult male giraffe life-history strategy is to roam among female herds in search of females in oestrus (Dagg, 2014). Interestingly, no such sex differences in home range sizes were evident using MCP (minimum convex polygon) methods in our study and in most other studies of giraffes, with the exception of populations in Namibia and Zambia (Table 1), providing further evidence that MCP methods may be less accurate than kernel estimators (Börger et al., 2006). Sex was not a significant predictor of home range size in our linear models, but this is likely due to the small sample size of adult males who had robust, stabilized home range estimates ($N = 4$). Thus, our inference about correlates of home range size at the ecosystem scale should extend to adult females only.

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Börger et al. (2006) demonstrated that most variation in home range size within a study population is due to differences between individuals, regardless of the estimation method used, and recommended increasing the number of individuals tracked at the expense of obtaining more locations per individual. The relatively large sample of 132 individual giraffes whose 95% kernel UD estimates stabilized suggests that our methods and data were appropriate for testing general patterns of home range sizes in our study area. Individuals whose home range sizes stabilized over the study period might nevertheless differ in other aspects of their behaviour from those of the remaining population, by being more dominant during access to food or being more sedentary.

<H1>Africa-wide Home Range Comparisons

Home range sizes of giraffes in the Tarangire-Manyara study area were generally smaller than in other regions of Africa, although home range estimates among studies were highly variable (Table 1). One potential factor driving variation in home range size among study populations across the African continent could be differences in rainfall and the availability of surface water (Deacon & Smit, 2017). We found that mean annual rainfall in a study area explained 74% of the variation in mean MCP home range size of giraffes. The smallest recorded giraffe home range sizes were in Lake Manyara National Park, and annual precipitation was relatively higher in Lake Manyara National Park than in all the other study areas (Table 1). In the most arid study area, the Namib desert, giraffe home range sizes reached up to 1900 km^2 (giraffe bull), which may be correlated with low forage density, increased searching for females and low giraffe population density (Fennessy, 2009).

The relationship we documented between rainfall and space use by a large herbivore is not surprising, given that rainfall mediates primary productivity (food resource availability) which in

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turn mediates space use by ungulates (McNaughton, 1985; McNaughton et al., 1988). The negative correlation we observed between space use by giraffes and rainfall—and therefore productivity—at the continent-wide scale reflects a similar pattern as that of home range size and distance from towns at the ecosystem scale: the greater the availability and access to critical resources such as food and water, the smaller the home range. Human disturbance and fragmentation of habitat in and around densely populated areas likely reduced the local forage and water resources available for giraffes, forcing individuals to increase their movements and use of space to obtain these resources. Similarly, lower primary productivity forces individuals to range more widely (Fennessey, 2009).

<H2>MCP Versus Kernel Estimators

Most previous published estimates of giraffe home range sizes used minimum convex polygon methods to calculate area (Table 1). Unfortunately, the MCP method has been found to be highly inefficient and biased, especially for small sample sizes of individuals and relocations (Börger et al., 2006). Minimum convex polygons provide only crude outlines of the range, are sensitive to extreme data points ("occasional sallies" as defined by Burt, 1943), fail to take into account information provided by the interior locations and approach asymptotic values of home range area only with large samples sizes (Powell, 2000). Whether to calculate home range sizes with minimum convex polygons or kernel utilization distribution depends on how the data were collected and on the research question (Börger et al., 2006; Fieberg & Börger, 2012). In our case, if surveys are conducted less frequently, there is a greater probability of missing detections at the edge of the range. Using MCP calculations could then lead to underestimation of the home ranges, which may underlie the much smaller MCP estimations in our study and others that compared MCP with kernel estimates using the same data (e.g. ocelots, *Leopardus pardalis*:

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Dillon & Kelly, 2008; African buffalo, *Syncerus caffer*: Ryan et al., 2006). MCP methods also failed to differentiate between larger home range sizes of males than females that were observed with kernel density estimates (Dillon & Kelly, 2008). For smaller sample sizes the kernel UD is likelier more robust. Nevertheless, for both methods a minimum number of data points per individual is needed to obtain an accurate estimation of the home range size (Börger et al., 2006). Therefore, we suggest utilizing home range estimates from individuals with a minimum number of relocations required for unbiased estimation, either by using a bootstrap procedure or another method, and when possible consider using kernel density estimators while taking into account barriers to movement.

<H2>Conclusions

Our study supports the hypothesis that home range sizes of large herbivores vary with access to or availability of resources. Furthermore, access or availability was influenced by anthropogenic factors. We found that 10% of the adult giraffes analyzed had stable home range sizes over a period of 6 years, and that those stable home ranges did not differ significantly in size from those of the remainder of the population. This may suggest that giraffes, instead of modifying the size of their home range, may move to areas of better suitability, a phenomenon that we did not address here. Nevertheless, in areas characterized by intensive human disturbance (but not in traditional pastoralist areas), adult female giraffes consistently roamed over larger areas at the landscape scale. At the continent-wide scale, primary productivity as indexed by rainfall mediated home range sizes of adult giraffes. Our results should help wildlife managers make informed decisions that improve conservation plans for at-risk species such as giraffes.

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Table 1

Mean (+SD) home range sizes of female and male giraffes, *Giraffa camelopardalis*, methods, sample sizes, geographical locations (NP = National Park) and mean annual precipitation from this study and reported in the literature

	Mean (SD) home range size (km^2)			Data collection method	Home range calculation method	Number of giraffes	Geographical location	Annual rainfall (mm)
	Females	Males	Both					
Masai giraffe, *G. c. tippelskirchi*								
	110.4 (54.9)	126.2 (67.9)	111.2 (55.3)	CMR[1]	95% Kernel UD	71	Tarangire NP, Manyara Ranch, Tanzania[2]	
	110.7 (24.6)	144.1 (27.4)	118.0 (28.4)	CMR	95% Kernel UD	37	Lake Manyara NP, Tanzania[2]	
	27.8 (23.2)	26.1 (17.6)	27.7 (22.8)	CMR	MCP 100%	71	Tarangire NP, Manyara Ranch, Tanzania[2]	650[12]
	12.5 (7.9)	19.8 (8.2)	14.0 (8.4)	CMR	MCP 100%	37	Lake Manyara NP, Tanzania[2]	915[13]
	9	5		CMR	Periphery method	~40	Lake Manyara NP, Tanzania[5]	
	85	62		CMR	MCP 100%	20	Nairobi NP, Kenya[3]	844[13]
	162	164	163	CMR	MCP 100%	110	Tsavo NP, Kenya[4]	553[13]
South African giraffe, *G. c. giraffa*								
	282			Radiocollar	MCP 100%	1	Kruger NP, South Africa[6]	312–650[13]

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	177 (wet) 245 (dry)		Satellite GPS	MCP 95%	8	Khamab Kalahari Nature Reserve, South Africa[7]	333[7]
Angolan giraffe, *G. c. angolensis*							
	200	514	CMR and radiocollar	MCP 100%	60	Namib desert, Namibia[8]	13–100[8]
West African giraffe, *G. c. peralta*							
	50 (wet) 103 (dry)	32 (wet) 134 (dry)	CMR	MCP 100%	28 (wet) 17 (dry)	Sahel, Niger[9]	400–600[9]
Reticulated giraffe, *G. c. reticulata*							
	64	96	CMR	Kernel UD 75%	160	Ol Pejeta Conservancy, Kenya[10]	739[14]
Thornicroft's giraffe, *G. c. thornicrofti*							
	68	82	CMR	MCP 100%	27	South Luangwa NP, Zambia[11]	<500[15]

[1] Capture–mark recapture.
[2] This study.
[3] Foster and Dagg (1972).
[4] Leuthold and Leuthold (1978).
[5] van der Jeugd and Prins (2000).
[6] du Toit (1990).
[7] Deacon and Smit (2017).
[8] Fennessey (2009).
[9] Le Pendu and Ciofolo (1999).

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[10] VanderWaal et al. (2014).
[11] Berry (1978).
[12] Foley and Faust (2010).
[13] Coe et al. (1976).
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[15] Bishop et al. (2016).

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Table 2

Model selection results from 14 linear regression models showing top-ranked five models explaining variation in 95% kernel utilization distribution home range sizes of 71 giraffes (67 females and 4 males) in the Tarangire-Manyara Ecosystem, based on maximum likelihood estimation

Model	Intercept	Bomas[1]	Towns[2]	PopDen[3]	Survey routes[4]	Sex	Veg1[5]	Veg2[6]	Veg3[7]	Veg4[8]	PopDen *sex	Towns *sex	*K*	AIC_c	ΔAIC_c	w_i
m 3	5.34	—	-0.08	—	-0.83	—	—	—	—	—	—	—	3	108.46	0.00	0.44
m 12	4.92	—	-0.11	—	—	—	—	—	—	—	—	—	2	110.21	1.75	0.18
m 1	5.83	-0.06	-0.10	-0.20	-0.90	0.30	—	—	—	—	—	—	6	110.36	1.91	0.17
m 11	4.86	—	-0.10	—	—	1.06	—	—	—	—	—	-0.17	4	110.43	1.97	0.16
m 7	5.36	—	—	—	-1.29	—	—	—	—	—	—	—	2	113.24	4.78	0.04

Models shown here are those that carried 99% weight. ΔAIC_c is the difference in AIC_c values between a model and the top-ranked model. *K* is the number of parameters in a model. w_i is model AIC_c weight, a metric for strength of evidence supporting a given model as the best description of the data.

[1] Distance (km) from edge of 100% MCP (minimum convex polygon) home range to nearest boma.

[2] Distance (km) from edge of 100% MCP home range to nearest town.

[3] Local giraffe population density.

[4] Density (km) survey routes in 95% kernel utilization distribution.

[5] Proportion Veg1 (*Acacia–Commiphora* deciduous bush-land and thicket) in 95% kernel utilization distribution.

[6] Proportion Veg2 (edaphic grassland on drainage-impeded or seasonally flooded soils) in 95% kernel utilization distribution.

[7] Proportion Veg 3 (edaphic grassland on volcanic soils with scattered woody species) in 95% kernel utilization distribution.

[8] Proportion Veg4 (*Acacia–Commiphora–Combretum* wooded grassland) in 95% kernel utilization distribution.

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Table 3

Model-averaged parameter estimates, standard errors, 95% confidence intervals and *P* values from multiple linear regression models explaining variation in home range size of 71 giraffes in the Tarangire-Manyara Ecosystem of northern Tanzania

Parameter	Estimate	SE	95% CI	*P*
(Intercept)	5.27	0.41	4.47 to 6.07	0.000
Routes	-0.57	0.54	-1.73 to -0.02	0.296
Towns	-0.09	0.04	-0.16 to -0.03	**0.019**
PopDen	-0.03	0.10	-0.54 to 0.13	0.740
Sex (M)	0.22	0.45	-0.42 to 1.77	0.620
Bomas	-0.01	0.05	-0.26 to 0.15	0.842
Towns*sex	-0.03	0.07	-0.36 to 0.02	0.706

Averages assume a variable is included in every model but in some models the corresponding coefficient and its variance is set to zero. Significant *P* values are shown in bold.

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Figure 1. Study area in the Tarangire-Manyara Ecosystem of northern Tanzania. White lines are roads and tracks surveyed for Masai giraffes, *G. c. tippelskirchii*, blue lines are rivers, light blue areas are alkaline lakes, green areas are national parks and conservancies, grey polygons are towns and points are bomas. LMNP = Lake Manyara National Park; TNP = Tarangire National Park; MRC = Manyara Ranch Conservancy; MGCA = Mtowambu Game Controlled Area; LGCA = Lolkisale Game Controlled Area.

Figure 2. Example of stabilization of giraffe home range estimates with the bootstrap procedure.

Figure 3. Visualizations of giraffe home ranges. Left: Male from Tarangire National Park. Right: Female from Lake Manyara National Park.

Figure 4. Log-transformed kernel home range sizes (km^2) of giraffes in the Tarangire-Manyara Ecosystem as a function of distance from developed areas (km).

Figure 5. Log-transformed minimum convex polygon (MCP) home range sizes (km^2) of giraffes as a function of annual rainfall (mm) from 10 study areas throughout Africa.

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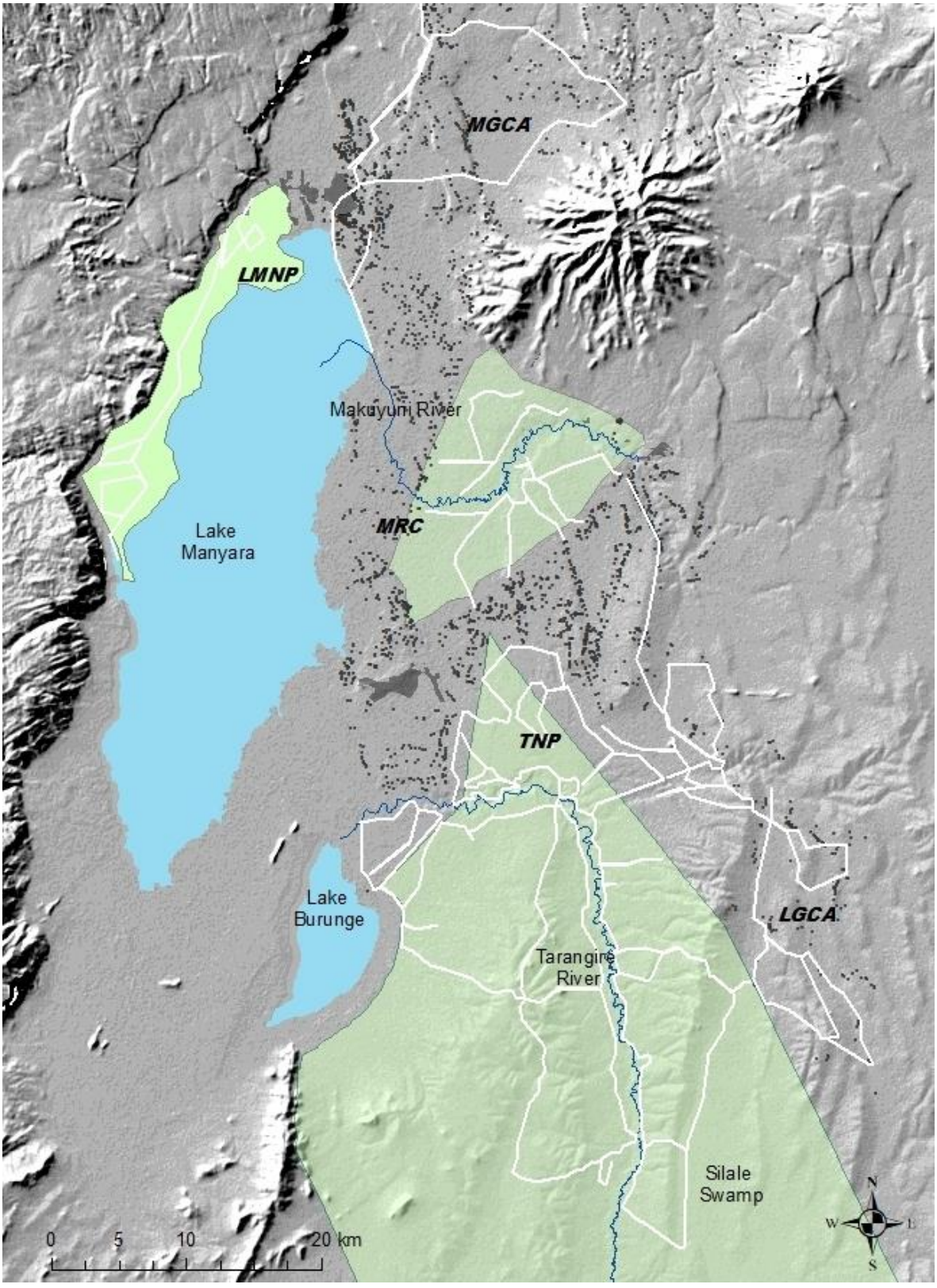
MGCA
LMNP
Makuyuni River
MRC
Lake
Manyara
TNP
Lake
Burunge
LGCA
Tarangire
River
Silale
Swamp
0
5
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20 km
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Figure 1.

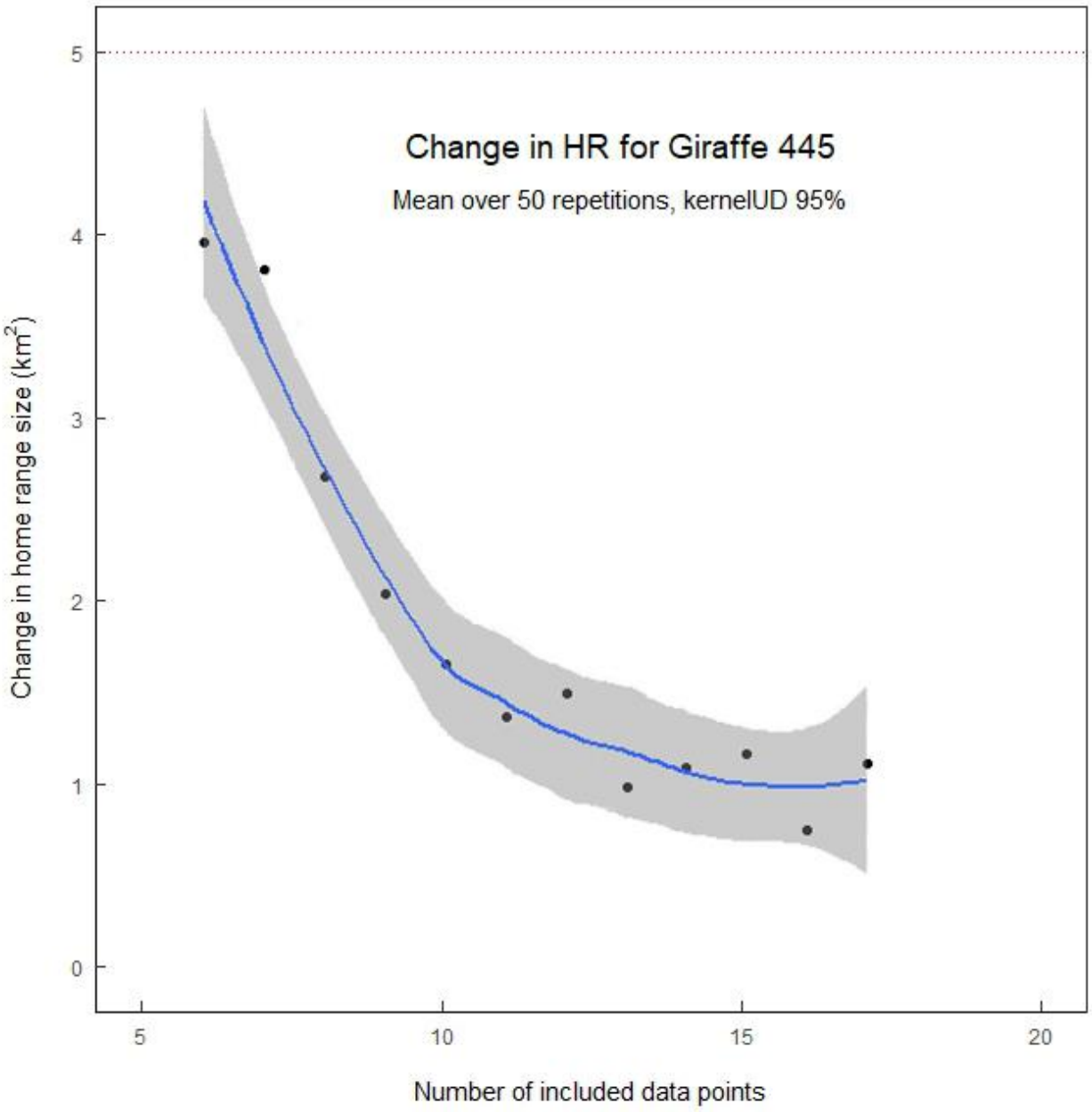
Change in HR for Giraffe 445
Mean over 50 repetitions, kernelUD 95%
Change in home range size (km^2)
Number of included data points
0
1
2
3
4
5
5
10
15
20

Figure 2.

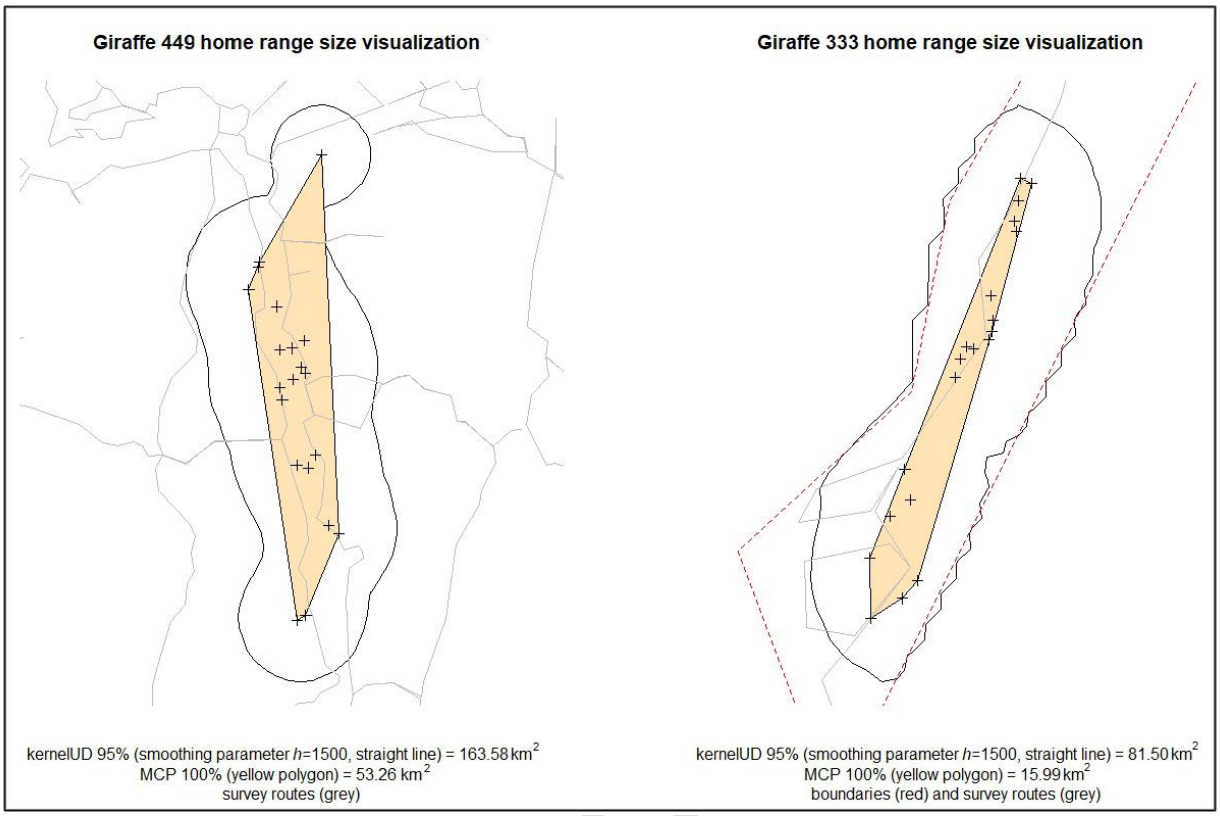

Figure 3.

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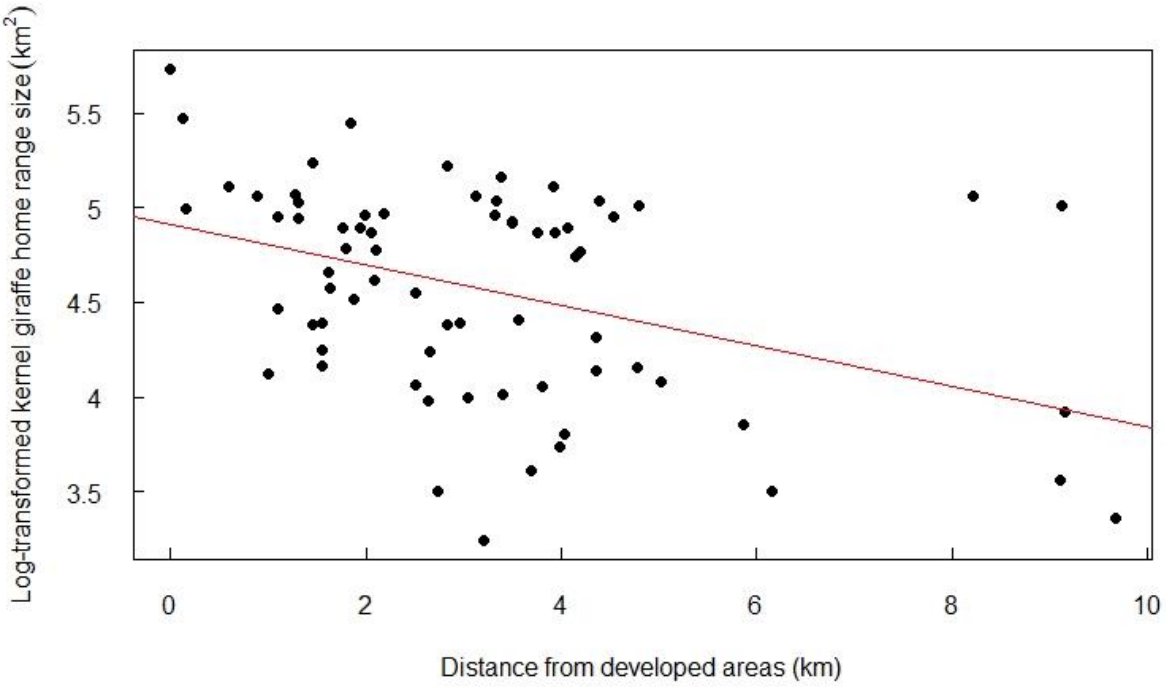

Figure 4.

Accepted

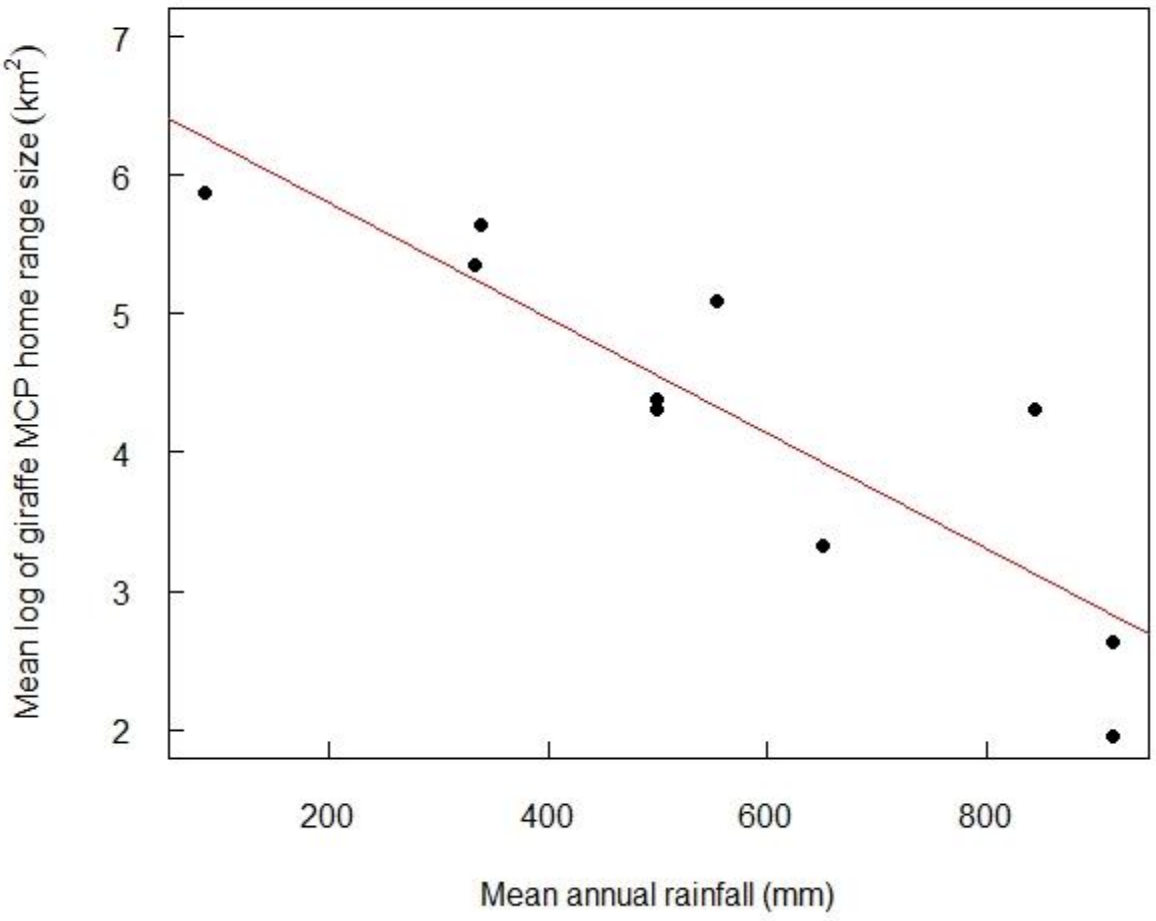

Figure 5.

Acce